Habitats Used by Juvenile Flagtails (*Kuhlia* spp.; Perciformes: Kuhliidae) on the Island of Hawai'i[1]

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Abstract: Patterns of juvenile habitat use by two species of kuhliid fishes (āholehole) on the island of Hawai'i were examined. *Kuhlia sandvicensis* was observed in marine habitat types only, but juvenile *K. xenura* were observed in freshwater streams, estuaries, on reef flats, along rocky shorelines, and in tide-pool habitats. Principal components analysis indentified nonrandom microhabitat selection by juvenile *K. sandvicensis* and *K. xenura*. Both species selected microhabitats that were higher in salinity and temperature and nearer to the open ocean than were areas randomly available to them. Although distributions of juvenile *K. sandvicensis* and *K. xenura* overlapped in marine habitats, characteristics of the marine microhabitats used by each species differed. Along rocky shorelines, *K. sandvicensis* used microhabitats that were characteristic of high-energy surge zones—deep areas close to the open ocean that had high salinities. The rocky shorelines most frequently inhabited by *K. xenura*, conversely, were shallower areas that were farther from the open ocean with lower salinity. A similar pattern was observed in tide-pool habitats, with *K. sandvicensis* using microhabitats typical of surge zones, and *K. xenura* utilizing protected tide pools with low salinities. Protection of a variety of inshore habitats is important for conservation of juvenile Hawaiian kuhliid fishes.

Fishes in the genus *Kuhlia* (the "flagtails") are found throughout the Indo-Pacific in marine, estuarine, and freshwater habitats. Known in Hawai'i as āholehole, they are highly sought-after food fishes and represent an important fishery. Āholehole were also culturally important to the ancient Hawaiian people and were often used in religious ceremonies (Titcomb 1972). Although two morphotypes (based primarily on eye size) had long been noted by local fishermen and biologists, before 2001 only one species, *Kuhlia sandvicensis* (Steindachner, 1876), was recognized in the scientific literature (Tester and Takata 1952, Gosline and Brock 1965, Tinker 1978, Randall 1985, 1996, Witte and Mahaney 1998). Randall and Randall (2001) published a revision of the genus that, based on meristic analysis, effectively "split" *K. sandvicensis* into two species. The "big-eyed" (colloquial) morphotype was assigned the available name *K. xenura* (Jordan & Gilbert, 1882), and this species is now believed to be endemic to the Hawaiian Islands. Meanwhile, the "small-eyed" morphotype, even though less frequently observed in what were formerly known as the Sandwich Islands, retained the name *K. sandvicensis*. Morphometric and genetic analyses of the two morphotypes provided confirmation that two species of *Kuhlia* occur in Hawaiian waters (McRae 2007). Although superficially similar, consistently observable differences in appearance exist between these two species. For example, the big-eyed *K. xenura* (or Hawaiian Flagtail) is deeper bodied and has finer and less-conspicuous reticulations on the head and

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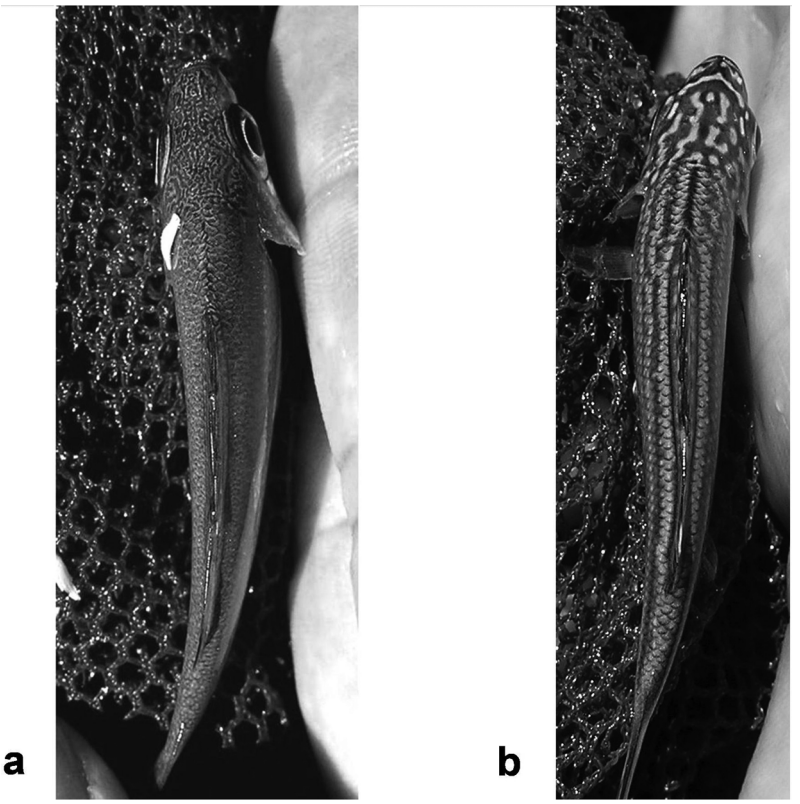

FIGURE 1. Vermiculated pattern on the dorsal surface of (*a*) *Kuhlia xenura* and (*b*) *Kuhlia sandvicensis* (from McRae 2007).

dorsal surface compared with the small-eyed *K. sandvicensis* (hence the common name Zebra-head Flagtail) (Figure 1).

It is not known whether information on the ecology and behavior of Hawaiian *Kuhlia* obtained before Randall and Randall's (2001) taxonomic revision (e.g., Tester and Takata 1953, Gosline 1965, Hosaka 1973) included observations on *K. sandvicensis*, *K. xenura*, or both species. Juvenile *K. xenura* have been documented to use riffles and runs in the terminal reach of Wailoa Stream on the island of Hawai'i as juvenile habitat (M.G.M., unpubl. data). Strontium/calcium profiles in the otoliths of *K. sandvicensis* and *K. xenura* indicated that both species experienced exposure to full-strength seawater and to water of reduced salinity during the life of individual animals (Benson and Fitzsimons 2002). To date, however, detailed analyses of the ecological similarities and differences between these two species are lacking.

The goal of this study was to compare both macro- and microhabitat use by juveniles of both kuhliids in Hawai'i to gain insight into the spatial ecology of these commercially and recreationally important species. The critical role of juvenile habitats in the survival and recovery of fish populations around the world has been well established (e.g., Rozas and Hackney 1983, Jennings 1992, Whitfield 1997, Desmond et al. 2000, Hendon et al. 2001). To obtain crucial ecological information that may aid in the management of āholehole in the Hawaiian Islands, the following null hypotheses were tested: (1) juvenile *K. sandvicensis* and *K. xenura* were utilizing the same habitat types (e.g., tide pools, streams,

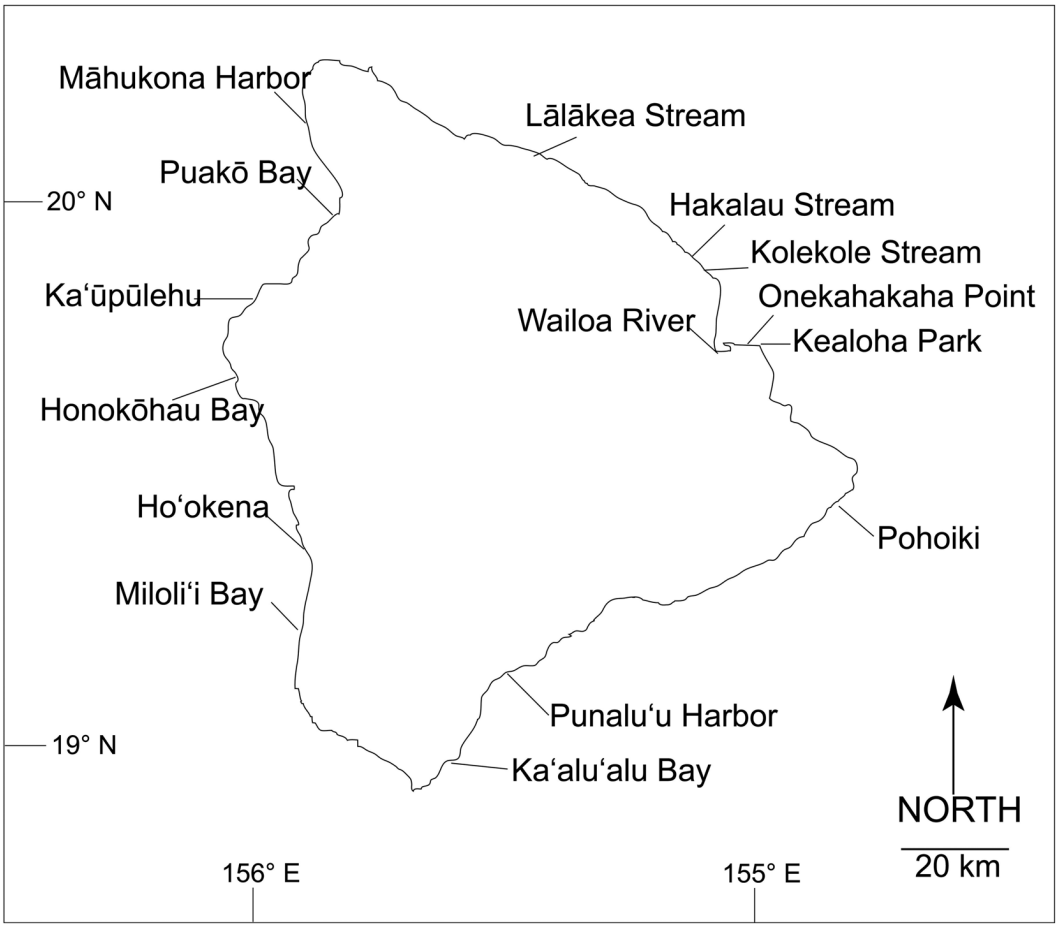

FIGURE 2. Survey sites on the island of Hawai‘i.

etc.) on the island of Hawai‘i; (2) the microhabitats utilized by *K. sandvicensis* and *K. xenura* on the island of Hawai‘i were not significantly different from the range of microhabitat conditions that were randomly available to them; and (3) in habitat types where both species occurred together, no partitioning of spatial resources was taking place.

MATERIALS AND METHODS

Field Methods

Study sites were located along all coastlines of the island of Hawai‘i and were selected based on accessibility and because they encompassed all the freshwater, estuarine, and marine habitat types in which juvenile *Kuhlia* have been observed in Hawai‘i (Figure 2). Marine habitat types surveyed included rocky shorelines, tide pools, and reef flats. Estuarine habitat types consisted of mixohaline terminal stream reaches and a brackish-water fishpond. Stream reaches far enough inland to not be influenced by tidal influx of salt water were the only freshwater habitats surveyed. Fish habitat use and random habitat availability data were collected during January, March, and May of 2004. A random numbers table was used to select the starting points of surveys

near shoreline or stream access points. While facing the water at the shoreline (or stream bank), the farthest visible point on the shoreline to the left was designated as 0%, and the farthest visible point to the right was designated as 100%. A random number of 65, for example, would result in a survey that started at a point that was located approximately 65% between the two farthest visible points. Surveys included all areas containing potential habitats along a 50–100 m length of shoreline (or stream reach) to the right or left of the randomly located starting point. Survey direction alternated between surveys. Fish were located visually either from the surface by using polarized glasses or during underwater snorkel surveys. All juvenile *Kuhlia* located were identified to species, counted, and their fork lengths (FL) were estimated. *Kuhlia* were considered to be juveniles if they were less than 15 cm FL (Tester and Takata 1953). The exact location of each individual or group of undisturbed *Kuhlia* was marked with a flagged fishing weight. Although the two species could be distinguished visually, fish were collected periodically to verify species identifications and length estimates.

The habitat type in which fish were observed was recorded (stream, estuary, rocky shoreline, tide pool, or reef flat), and the distance from the open ocean (as indicated by observable wave surge) was either measured by using a 100 m tape measure or visually estimated. For survey sites located in stream reaches, the distance from the open ocean was estimated by using a topographical map and a digital map wheel (Scalex). At each marked fish location, salinity, temperature, and dissolved oxygen were measured with a multiprobe (YSI). Depth and mean water column velocity were measured using a top-set wading rod and an electromagnetic flow meter (Marsh-McBirney Flo-Mate 2000). To characterize microhabitat availability at each study site, a random number table was used to select 30–50 points within the survey area. At each of these random points, measurements were made on the same set of variables that were measured for the marked fish locations. The total area of each habitat type surveyed was estimated by subdividing each surveyed habitat into rectangular and triangular sections, and using a 100 m tape measure to measure the length and width of each subsection.

Statistical Analysis

SYSTAT 8.0 (SPSS Inc. 1998) was used to perform all statistical tests. To examine whether or not the juveniles of the two species of *Kuhlia* were utilizing the same habitat types on the island of Hawai'i, population densities for each species were calculated for each habitat type. For each survey site, the total number of fish observed in each habitat type was divided by the total area (square meters) of that habitat type present. Mann-Whitney *U*-tests (nonparametric analog of the two-sample *t*-test) were performed to test for significant differences between the mean population densities (number $\cdot$ m^{-1}) of the two species in each habitat type.

To test for nonrandom microhabitat selection by *K. sandvicensis* and *K. xenura*, a Principal Components Analysis (PCA) was conducted on the random availability data. Before running the PCA, data for variables that displayed excessive skewness or kurtosis were transformed as necessary with either a square root or a fourth root transformation. The PCA (based on the correlation matrix with a Varimax rotation) extracted independent component axes that described patterns of microhabitat variation within surveyed habitats. Observations of fish microhabitat use were scored and superimposed on the component axes by multiplying each fish's microhabitat use data by the eigenvectors associated with the microhabitat variables on each component axis (Grossman and Freeman 1987). Two-sample Kolmogorov-Smirnoff (KS) tests were used to examine whether or not the frequency distribution of each species' principal component scores were significantly different in shape from those of the habitat availability scores.

To test for interspecific differences in microhabitat use in habitat types where they occurred together, the mean values of microhabitat variables observed for both species were compared by using Mann-Whitney *U*-tests.

RESULTS

A total of 152 juvenile *K. sandvicensis* (15–82 mm FL) and 707 juvenile *K. xenura* (12–123 mm FL) was observed. Juvenile *K. xenura* were found in every habitat type surveyed. Although *K. xenura* was more commonly encountered in most habitat types surveyed, their densities were not significantly higher than those observed for *K. sandvicensis* except for in streams and estuaries, where *K. sandvicensis* was not observed (Table 1). Mann-Whitney *U*-tests for differences between the population densities of the two species were, consequently, significant at the $\alpha = .05$ level for the stream ($U = 2.5$, $P = .02$) and estuary ($U = 0$, $P = .01$) habitat types only (Table 1). The first null hypothesis, which stated that juvenile *K. sandvicensis* and *K. xenura* were utilizing the same habitat types on the island of Hawai'i was therefore rejected.

Our second null hypothesis, stating that the microhabitats utilized by *K. sandvicensis* and *K. xenura* on the island of Hawai'i were not significantly different from the range of microhabitat conditions that were randomly available to them, was also rejected. The PCA performed on the microhabitat availability

TABLE 1

Total Area of Each Habitat Type Surveyed, with Associated Population Densities and Site Information, Sample Sizes (Number of Individual Survey Sites in Each Habitat Type), Mann-Whitney Test Statistic (*U*), and Associated *P*-Values

Habitat (m^2)	Site (m^2)	No. per m^2 ± Standard Error		
		K. xenura	*K. sandvicensis*	*n*, *U*, *p*-Value[a]
Stream (1,054)	Hakalau (88) Kolekole (50) Lālākea (916)	0.27 ± 0.17	0	5, 2.5, .02*
Estuary (219)	Hakalau (70) Kolekole (60) Wailoa River (89)	0.44 ± 0.14	0	4, 0, .01*
Reef flat (4,156)	Honokōhau Bay (2,517) Ho'okena (871) Ka'ūpūlehu (396) Miloli'i Bay (75) Puakō Bay (296)	0.02 ± 0.01	0.01 ± 0.004	5, 9, .45
Rocky shoreline (1,717)	Ka'alu'alu Bay (594) Ka'ūpūlehu (30) Kealoha (131) Māhukona Harbor (144) Miloli'i Bay (34) Onekahakaha Point (484) Pohoiki (217) Puakō Bay (45) Punalu'u Harbor (38)	0.11 ± 0.07	0.16 ± 0.16	11, 77, .19
Tide pool (1,194)	Honokōhau Bay (3) Ho'okena (11) Ka'alu'alu Bay (15) Ka'ūpūlehu (99) Māhukona Harbor (16) Miloli'i Bay (496) Onekahakaha Point (146) Pohoiki (30) Puakō Bay (338) Punalu'u Harbor (41)	1.77 ± 1.52	0.2 ± 0.11	13, 61, .21

[a] An asterisk (*) identifies comparisons where the densities of the two species in a particular habitat type were significantly different.

TABLE 2

Rotated Loading Values for Microhabitat Variables on Each Principal Component (PC) Axis

Microhabitat Variable	PC1	PC2
Temperature	–0.84	–0.30
Dissolved oxygen	0.31	–0.77
Salinity	–0.89	0.12
Distance to open ocean	0.71	–0.16
Mean water column velocity	–0.05	0.79
Depth at fish	0.17	0.45

data ($n = 172$) produced two component axes that explained 61.4% of the total variance in the data set. Microhabitat variables with high loading values on Principal Component (PC) axis 1 were temperature, salinity, and distance to the open ocean; dissolved oxygen, mean water column velocity, and depth at fish had high loading values on PC axis 2 (Table 2, Figure 3). Juvenile *K. sandvicensis* ($n = 152$) showed strongly nonrandom microhabitat use on PC axis 1 ($P < .0005$ [Figure 3]): they selected microhabitats that were higher in salinity and temperature, and closer to the open ocean than were randomly available (Table 3, g and h). *Kuhlia sandvicensis* juveniles also displayed nonrandom ($P < .0005$) microhabitat use with respect to PC axis 2 (Figure 3). They utilized relatively deep areas with lower levels of dissolved oxygen and lower water velocity than were randomly available on the island of Hawai'i (Figure 3; Table 3, g and h). *Kuhlia xenura* juveniles showed nonrandom microhabitat use on PC axis 1 ($P < .0005$) but not on PC axis 2 ($P = .16$ [Figure 3]). Juvenile *K. xenura* selected microhabitats that were higher in salinity and temperature, and closer to the open ocean than were randomly available (Figure 3; Table 3, g and h). The distributions of principal component scores for *K. xenura* on PC axis 2 were not significantly different from the distribution of scores for random microhabitat availability ($P = .16$ [Figure 3]).

Finally, the third null hypothesis, which stated that no microhabitat partitioning was taking place between juveniles of the two species in habitat types where they co-occur, was rejected. In marine sites, the use of microhabitats differed between *K. sandvicensis* and *K. xenura* (Table 3, f). *Kuhlia sandvicensis* generally used marine microhabitats that were lower in dissolved oxygen, of higher salinity, located nearer to the open ocean, and higher in water velocity than were the microhabitats used by *K. xenura* (Table 3, f). Mann-Whitney *U*-tests indicated significant differences between the two species with respect to the means of the microhabitat observations measured along rocky shorelines (except for mean water column velocity) and in tide pools (except for temperature and depth at fish) but not on reef flats (except for dissolved oxygen [Table 3, c–e]).

DISCUSSION

The results presented here indicate that *K. sandvicensis* utilized a narrower range of habitats during the juvenile stage than did *K. xenura*. The most notable results were that juvenile *K. sandvicensis* were only observed in marine habitat types and were never observed at the estuary sites or in freshwater streams during this study. Juvenile *K. xenura*, conversely, were found in every marine, estuarine, and freshwater habitat surveyed. In marine habitat types where the two species occurred together, *K. xenura* generally used areas that were farther from the open ocean than did *K. sandvicensis*. During this study, it was not uncommon to observe schools of juvenile *K. xenura* inhabiting the most protected areas of rocky shorelines, while juvenile *K. sandvicensis* were observed in the turbulent surge zones along the same shorelines. A similar pattern was observed in tide pools where the two species overlapped in their distributions. In tide-pool habitats, juvenile *K. sandvicensis* were commonly observed within or very near high-energy surge zones that were higher in salinity and water velocity. Conversely, the areas of tide pools inhabited by *K. xenura* were brackish and protected from wave surge such that water velocities were low.

The habitat-use patterns described here for Hawai'i's kuhliid fishes correspond to broader patterns in their biogeography. *Kuhlia sandvicensis* has been recorded from

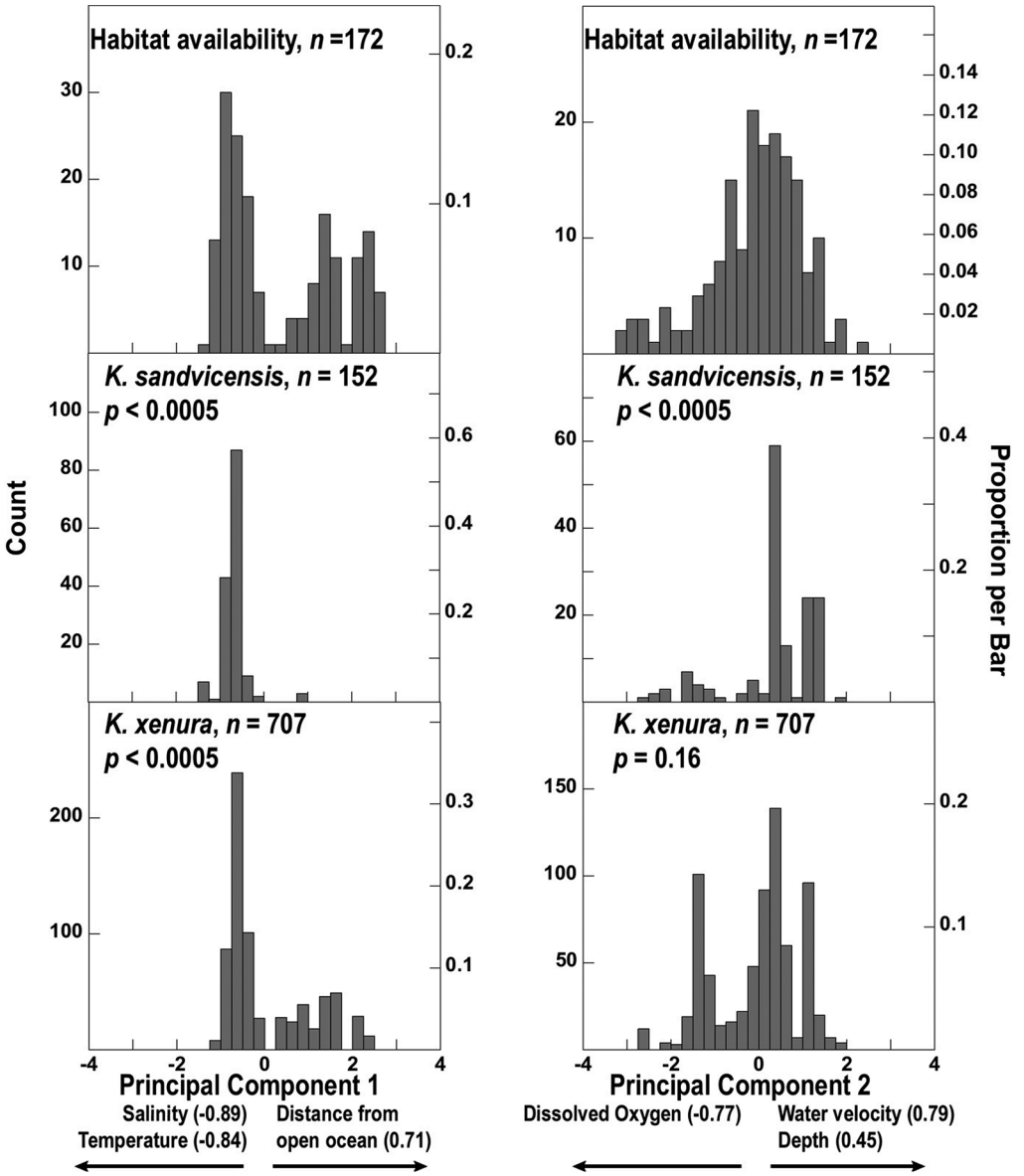

FIGURE 3. Tests of nonrandom microhabitat use for Principal Component Axes 1 and 2. Diagrams represent distributions of component scores for both microhabitat availability and species use data. Numbers in parentheses are component loading values for the variables represented by each axis. Microhabitat variables with loading values ≥0.40 were included in the analysis. Two-sample Kolmogorov-Smirnoff tests were used to calculate *P*-values.

Indo-Pacific islands outside the Hawaiian archipelago where freshwater habitats are rare or nonexistent (e.g., Johnston Island [Randall and Randall 2001]). *Kuhlia xenura* is endemic to the Hawaiian Islands (Randall and Randall 2001), where the presence of streams, rivers, and submarine freshwater springs (Street et al. 2007) result in an abundance of

TABLE 3

Microhabitat Variable Means (± Standard Error) for Juvenile *Kuhlia* Observed, with Mann-Whitney Test Statistic (*U*) and Associated *P*-Values

Variable	*K. sandvicensis*	*K. xenura*	*U*, *P*-Value
(a) Stream	(0)	(97)	
Temperature (°C)	n.o.	23.33 ± 0.119	
Dissolved oxygen (mg liter^{-1})	n.o.	9.16 ± 0.074	
Salinity (ppt)	n.o.	0.031 ± 0.002	
Distance to open ocean (m)	n.o.	401.48 ± 50.41	
Mean water column velocity (m sec^{-1})	n.o.	0.173 ± 0.022	
Depth at fish (cm)	n.o.	46.41 ± 3.07	
(b) Estuary	(0)	(92)	
Temperature (°C)	n.o.	22.87 ± 0.068	
Dissolved oxygen (mg liter^{-1})	n.o.	9.36 ± 0.030	
Salinity (ppt)	n.o.	1.40 ± 0.200	
Distance to open ocean (m)	n.o.	8.21 ± 35.98	
Mean water column velocity (m sec^{-1})	n.o.	0.136 ± 0.016	
Depth at fish (cm)	n.o.	71.93 ± 2.21	
(c) Reef flat	(59)	(135)	
Temperature (°C)	26.80 ± 0.086	27.02 ± 0.091	3527.5, .08
Dissolved oxygen (mg liter^{-1})	8.73 ± 0.099	8.86 ± 0.083	3463.5, .05
Salinity (ppt)	33.51 ± 0.186	33.28 ± 0.172	4052.0, .77
Distance to open ocean (m)	11.69 ± 1.92	13.17 ± 1.28	3495.5, .06
Mean water column velocity (m sec^{-1})	0.111 ± 0.005	0.115 ± 0.005	4036.5, .84
Depth at fish (cm)	54.86 ± 2.04	51.60 ± 1.45	4427.5, .09
(d) Rocky shoreline	(27)	(101)	
Temperature (°C)	26.36 ± 0.065	23.75 ± 0.119	2668.5, <.0005
Dissolved oxygen (mg liter^{-1})	7.29 ± 0.124	8.18 ± 0.074	328.5, <.0005
Salinity (ppt)	33.72 ± 0.712	24.27 ± 0.481	2569.5, <.0005
Distance to open ocean (m)	0.889 ± 0.062	43.13 ± 5.04	972.0, .02
Mean water column velocity (m sec^{-1})	0.236 ± 0.023	0.243 ± 0.018	114.5, .16
Depth at fish (cm)	61.98 ± 1.13	43.49 ± 2.01	2064.0, <.0005
(e) Tide pool	(66)	(282)	
Temperature (°C)	26.99 ± 0.209	27.15 ± 0.116	8680.5, .39
Dissolved oxygen (mg liter^{-1})	8.10 ± 0.168	8.68 ± 0.064	7051.0, <.0005
Salinity (ppt)	30.00 ± 0.860	27.42 ± 0.511	10714.0, .01
Distance to open ocean (m)	12.77 ± 2.44	10.27 ± 0.382	6969.5, <.0005
Mean water column velocity (m sec^{-1})	0.201 ± 0.023	0.077 ± 0.007	13212.0, <.0005
Depth at fish (cm)	39.30 ± 2.69	41.19 ± 0.945	8783.0, .47
(f) Marine habitat types only	(152)	(518)	
Temperature (°C)	26.81 ± 0.098	26.45 ± 0.091	40903.5, .46
Dissolved oxygen (mg liter^{-1})	8.20 ± 0.094	8.63 ± 0.045	28120.0, <.0005
Salinity (ppt)	32.02 ± 0.424	28.42 ± 0.323	49201.0, <.0005
Distance to open ocean (m)	10.24 ± 1.34	17.48 ± 1.20	28308.0, <.0005
Mean water column velocity (m sec^{-1})	0.173 ± 0.012	0.120 ± 0.006	48013.0, <.0005
Depth at fish (cm)	49.37 ± 1.60	44.51 ± 0.775	48631.5, <.0005
(g) All habitat types combined	(152)	(707)	
Temperature (°C)	26.81 ± 0.098	25.56 ± 0.089	69103.5, <.0005
Dissolved oxygen (mg liter^{-1})	8.20 ± 0.094	8.80 ± 0.036	32039.0, <.0005
Salinity (ppt)	32.02 ± 0.424	21.01 ± 0.520	77929.0, <.0005
Distance to open ocean (m)	10.24 ± 1.34	99.43 ± 8.26	28308.0, <.0005
Mean water column velocity (m sec^{-1})	0.173 ± 0.012	0.129 ± 0.006	63859.5, <.0005
Depth at fish (cm)	49.37 ± 1.60	48.34 ± 0.839	58655.0, .08
(h) Availability measurements: All habitat types combined	(172)		
Temperature (°C)	24.61 ± 0.191		
Dissolved oxygen (mg liter^{-1})	9.02 ± .095		
Salinity (ppt)	18.86 ± 1.13		
Distance to open ocean (m)	207.71 ± 26.09		
Mean water column velocity (m sec^{-1})	0.234 ± .020		
Depth at fish (cm)	41.36 ± 2.82		

Note: Numbers in parentheses indicate sample size; n.o., not observed. No *K. sandvicensis* were observed in streams and estuaries, therefore Mann-Whitney test statistics could not be calculated for data collected in those habitat types.

low-salinity habitats. The theory of limiting similarity (MacArthur and Levins 1967) predicts that between two competing species, a maximum amount of overlap in ecological niche space exists, above which one species will be excluded (Abrams 1983). The ability of *K. sandvicensis* and *K. xenura* to coexist in the Hawaiian Islands despite being closely related and morphologically similar is likely facilitated by marked differences in their spatial ecology as juveniles.

Juvenile *K. sandvicensis* have distinct morphological adaptations that may facilitate survival in high-energy surge zones. *Kuhlia sandvicensis* is less deep-bodied than *K. xenura* (McRae 2007), resulting in a more hydrodynamically efficient profile that may enhance their ability to maintain their position in high water velocity areas. The pattern of dark vermiculated lines present along the dorsal and upper lateral surfaces of juvenile *K. sandvicensis* (Figure 1) provides camouflage in turbulent, foamy waters (authors, pers. obs.) and may help them avoid marine predators.

It is important to emphasize that before Randall and Randall's (2001) reclassification of the kuhliids of the central Pacific, only one species, identified as *K. sandvicensis*, was believed to exist in the Hawaiian Islands. Previous descriptions of the habitats used by *K. sandvicensis* in the Hawaiian Islands (e.g., Tester and Takata 1953, Tinker 1978, Hoover 1993, Randall 1996, Yamamoto and Tagawa 2000), therefore, could have referred to either *K. sandvicensis*, *K. xenura*, or (most likely) both species. All of these descriptions state that *K. sandvicensis* inhabits freshwater, estuarine, and marine habitats, a pattern that has now been documented for *K. xenura*. The species now identified as *K. sandvicensis* has been shown in this study to utilize a much narrower range of habitats than *K. xenura* during their juvenile stage, a fact that may require unique management strategies to effectively conserve this species.

Many questions regarding the ecology of kuhliid fishes in Hawai'i remain to be addressed in future studies. For example, are observed differences in the habitats used by juvenile *K. sandvicensis* and *K. xenura* due to physiological limitations leading to differences in salinity tolerance? Are juvenile *K. sandvicensis* and *K. xenura* utilizing similar food resources in habitats where they co-occur? Beck et al. (2001) defined nursery habitats as subsets of juvenile habitats that make a greater than average contribution to the adult population. Future investigations that focus on identifying which of the juvenile habitats outlined here represent true nurseries for Hawaiian kuhliids will provide fisheries managers in Hawai'i with ecological information that will enhance their ability to effectively manage these important indigenous fishes.

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